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Feed intake in channel catfish: is there a genetic component?

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Abstract

Increasing catfish growth is a primary objective of our broodstock improvement programme, and growth is at least partly dependent on voluntary feed intake. Two experiments were conducted to determine the genetic component of feed intake, and the relationship between feed intake and growth in sib-groups of channel catfish. In the first experiment, 10 fish from each of 31 full-sib families from the USDA-103 strain of channel catfish, *Ictalurus punctatus* (Rafinesque), were individually identified with passive integrated transponder (PIT) tags and distributed into two replicate tanks, five fish from each family to each tank. Fish were fed to apparent satiation with feed labelled with an X-ray opaque marker for one meal, radiographed, and feed intake was quantified for each individual. Genetic effects (broad sense heritability) accounted for approximately 41% of the phenotypic variation in feed intake. These fish were then grown for 5 months and the mean change in weight of the family groups was significantly correlated with mean feed intake ($r = 0.64$, $P < 0.001$). A subsequent experiment compared the feed intake of 100 families of catfish with their growth rate over the previous 2 months. Each family was grown in a separate 800 L tank. Fish were fed to apparent satiation daily and mean weight was determined monthly. After the 2 month growth period, fish were fed the labelled feed to apparent satiation, 28–30 individuals from each family/tank were radiographed, and individual feed intake was determined. A highly significant correlation ($r = 0.54$, $P < 0.0001$) between mean specific growth rate and mean feed intake (% consumption) was demonstrated. Taken together, these results suggest that individual feed intake has a heritable basis, and should be responsive to selection. Selection for increased feed intake could result in a correlated response of increased growth.

Keywords: feed intake, growth, correlated traits, heritability, channel catfish

Introduction

Animal growth is at least partly determined by feed availability and feed intake. Even under circumstances where feed is made available to near satiation levels, for example in some experimental and commercial culture conditions, differences in intake and growth persist due to variation between individuals (McCarthy, Houlihan, Carter & Moutou 1993), strain differences (Silverstein, Wolters & Holland 1999a) and environmental differences (Silverstein, Wolters, Shimizu & Dickhoff 2000). Growth of channel catfish, *Ictalurus punctatus* (Rafinesque), during the summer is often limited by the amount of feed distributed to the fish due to poor water quality, particularly low dissolved oxygen (Li, Robinson & Wolters 1998; Tucker & Robinson 1990), but spring and autumn growth appears to be limited by feed intake. One route to improving growth in cultured fishes would be to improve feed intake while maintaining feed efficiency.

Other meat animal industries have focused attention on feed intake as a means to improve

animal growth and quality traits (e.g. poultry, Chambers, Wang & McMillan 1994; swine, Johnson, Chewning & Nugent 1999; beef, Archer, Arthur, Herd, Parnell & Pitchford 1997). Selection for increased feed intake could result in similar improvements in production efficiency for fish.

Although it seems axiomatic that faster growing fish would eat more to support their growth, whether feed intake measured at one time would reflect growth potential is not known. A study designed to investigate environmental factors influencing the feeding activity of catfish in ponds showed that the amount of feed consumed the previous day had larger effects on feed consumption than daily temperature, dissolved oxygen and other environmental variables over a growing season (Taylor, Hargreaves, Tucker & Kingsbury 1999). This result suggests that the relationship between a one time measurement of feed consumption and growth may not be strong and should be carefully evaluated.

Measurement of amount of feed consumed by fish has largely been limited to groups of animals (Li & Lovell 1992; Thorpe, Talbot, Miles & Keay 1990; Robinson & Li 1996; Bellardi, Bianchini, Domenis & Palmegiano 1995; Silverstein & Shimma 1994). However, X-radiographic techniques for non-lethal measurement of feed intake in individuals have been developed and used reliably for over 20 years (Talbot & Higgins 1983). Measurement of feed intake by individuals enables the individual to be the experimental unit rather than a tank or pond of fish (Hurlbert 1984). This reduces the number of groups of fish that must be raised to estimate treatment effects. In previous work measuring feed intake of individual fish, we showed significant strain differences in feed intake and growth (Silverstein *et al.* 1999a). Estimation of within- and between-family variance is a prerequisite for estimating genetic variation for a trait using traditional quantitative genetic methods (Falconer 1986). As in all studies measuring voluntary feed intake, there is an inherent pitfall of not knowing if all fish eat to satiation. Social interactions between fish may influence feed intake, and the point at which feeding is terminated is somewhat arbitrary. Use of the labelled diet helps to overcome some of these difficulties because feed can be provided to excess and the amount of feed actually consumed by each fish measured accurately.

Genetic variation for feed intake and growth could be exploited for improvement of fish as it has been for other livestock industries. The present studies were done to evaluate the genetic variation for feed consumption during a single feeding bout and to examine the correlation between feed consumption and long-term measures of growth.

Materials and methods

Two experiments were conducted. The fish used in both experiments were from the USDA-103 strain of channel catfish. This strain of catfish has been under selective breeding at the USDA catfish genetics research unit in Stoneville, MS for three generations (Li *et al.* 1998). All feeding experiments were done indoors in 800 L circular tanks. Water supplied was flow-through well water supplemented with calcium (temperature of 26 °C, pH 8.6, dissolved oxygen >5.0 mg L^{-1}, total hardness 51.3–68.4 mg L^{-1} as $CaCO_3$).

For the first experiment 31 full-sib families, produced by a random mating population in 1998, were reared in separate tanks for one year and then tagged intramuscularly by injection of a passive integrated transponder (PIT) tag when they were approximately 50–100 g. After the fish had recovered from tagging, approximately 10 fish from each of the 31 families were divided into two 800 L tanks, five fish from each family in each tank. Fish were allowed to recover and acclimate to the new tanks, indicated by resumption of feeding, for 2 weeks. The fish were then starved for one day and on the following day the fish were fed to apparent satiation in one feeding with labelled feed (detailed below). Replicate tanks were fed the labelled diet and measured one day apart (23 and 24 June 1999). Approximately 2 h after feeding the fish were netted and quickly anaesthetized with tricaine methansulfonate (MS-222). Each fish was weighed, PIT tag number recorded, X-radiographed to measure the quantity of feed consumed, and returned to the 800 L tank. Subsequently these fish were moved, along with their siblings, to outdoor ponds for growth assessment and fed to apparent satiation daily. On 17 December 1999 these fish were harvested. Weights of the individuals that had been in the feed intake trial were measured.

In the second experiment, 100 full-sib families from the USDA-103 strain were reared in individual 800 L circular tanks. These families were produced by pond spawning and because there were more spawns than the number of males present in the ponds, we know that some of the families are related

as half-sibs. Analysis of polymorphic microsatellite markers enabled identification of the full and half-sib relationships (Waldbieser & Wolters 1999). These families were maintained in 80 L aquaria for hatching and initial rearing. All embryos hatched between 17 May and 4 July 1999. From each full-sib family, 300 fish were weighed and moved to the 800 L tanks on 3 and 4 August 1999. Subsequent weight measurements were made in September and October by measuring the total weight of all fish in the tank and dividing by the number of fish to calculate mean weight. Fish were not starved prior to measurement of feed intake on 18 and 19 October 1999. Labelled feed was delivered to each tank until the fish reached apparent satiation. Beginning 1 h after feeding the fish were netted and quickly anaesthetized with tricaine methansulfonate (MS-222), between 25 and 30 fish from each family were weighed and X-radiographed to estimate feed consumption. Fifty tanks were measured each day for 2 days.

Labelled feed was prepared as described in Silverstein *et al.* (1999a). Briefly, the commercial diet on which the fish had been fed (32% Protein, SF Services, Greenville, MS, U.S.A) was ground, leaded glass ballotini beads of 0.4–0.6 mm diameter (Sigmund Lindner GmBH, type H) were mixed into the meal at the rate of 1%, and the diet was repelleted with a pellet press. A standard curve for the number of radio-opaque particles was produced from radiographs of duplicate samples of 0.25, 0.5, 1.0, 2.0, 4.0 and 8.0 g of labelled feed. Radiographs were taken with a Soyee SY-31-90P (Soyee, South Korea) X-ray unit (settings were 20 mA, 50 kVp for 0.1 s, the film used was Dupont/Sterling UVL 100 speed, with an UV detail screen). Radio-opaque particles in the stomach were counted with Image Pro (Media Cybernetics, Silver Springs, MD), an image analysis program, and compared with the standard curve to estimate the weight of feed consumed.

Feed consumption was evaluated by two measures. The first measure was weight of feed consumed and it was analysed by analysis of covariance with body weight as the covariate. The second measure was % consumption [100 (feed consumed (g) body weight $(g)^{-1}$)]. The relationships between weight of feed consumed and % consumption with body size were investigated by regression analysis.

Growth was evaluated by three different measures, change in weight (*d*weight), specific growth rate for weight (G_w) and the growth index *a* (Jobling 1983; Silverstein *et al.* 1999a). For the first experiment, change in weight was simply the end weight (17 December 1999) minus the weight at the time of feed intake measurement. For specific growth rate, the formula $G_w = (\ln W2 - \ln W1)\ 100/t$ was used, where $W2$ is the weight at the end of the growth interval, $W1$ is the weight at the beginning of the growth interval and t is the number of days in the interval (176). The growth index a was calculated from the equation:

$$\log_e G_w = a - 0.371 \log_e W_m$$

where W_m is the mean within-tank weights during the feeding trial. W_m was calculated as: (mean within-tank weight at the start of the experiment + mean within tank weight at the end of the experiment)/2. Growth rate was also evaluated for the families in the second experiment. Because the families were of different ages and sizes over the intervals measured, only G_w and a were calculated for families in the second experiment.

Statistical analyses

To determine the genetic component of variation for feed consumption in the first study (31 families), the data were evaluated using the linear model :

$$Y_{ijk} = \mu + W_{ijk} + T_i + F_j + TF_{ij} + \varepsilon_{ijk}$$

Y_{ijk} is the dependent variable weight of feed consumed, μ is the grand mean, T_i is the random tank effect, F_j is the random family effect, TF_{ij} is the tank by family interaction, and ε_{ijk} is the random error term. Body weight, W, was used as a covariate. A mixed model procedure (PROC MIXED SAS Institute 1996) was used to estimate variance components due to tank, family and tank by family interactions. Genetic interpretation of the family and residual variance components followed Falconer (1986) and Becker (1984).

The relationships between feed intake and growth measures in the first experiment were examined by correlation analysis of % consumption with *d*weight, G_w and *a*. Correlations were determined for individual % consumption with individual growth measures, and for family means for % consumption with growth measures.

In the second experiment with 100 families, the relationship of family means for % consumption with G_w and *a* were examined by correlation analysis. Additionally, preliminary identification of

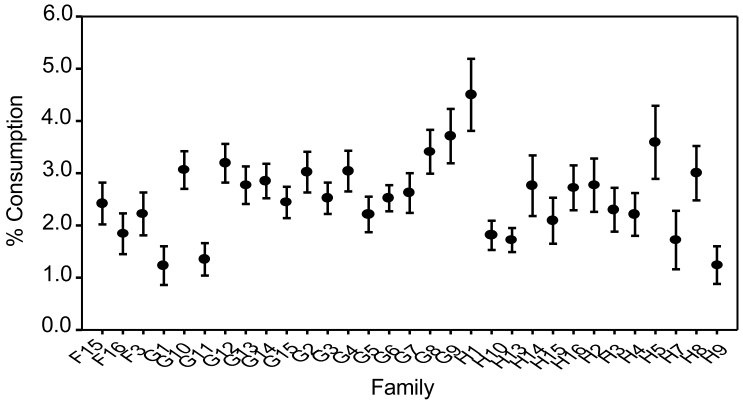

Figure 1 The mean % consumption for each family in experiment 1. Error bars represent standard error. The labels along the *X*-axis refer to the family coding.

Table 1 Descriptive statistics for the fish measured for feed intake in experiments 1 and 2. All fish radiographed for feed intake measurement were included (mean ± SD).

		Range
Experiment 1		
N	290	
Number of family groups	31	
Mean weight (g)	94.3 ± 38.3	34.5–280.2
Mean weight of feed consumed (g)	2.52 ± 1.81	0.00–9.10
% consumption	2.58 ± 1.44	0.00–9.40
*d*weight[1]	450.4 ± 79.7	290.5–656.5
G_w[2]	0.46 ± 0.05	0.33–0.54
a[3]	0.58 ± 0.05	0.41–0.68
Experiment 2		
N	3023	
Number of family groups	100	
Mean weight (g)	33.8 ± 14.6	3.0–104.7
Mean weight of feed consumed (g)	0.76 ± 0.87	0.00–6.63
% consumption	2.08 ± 2.09	0.00–9.86
G_w	1.68 ± 0.44	0.86–2.86
a	0.62 ± 0.14	0.31–0.92

[1]*d*weight is the change in weight from 24 June to 17 December 1999.

[2]G_w is the specific growth rate for weight defined as $(\ln W2 - \ln W1)\ 100/t$.

[3]*a* is a growth index defined as $\log_e G_w = a - 0.371 \ln W_m$.

14 half-sib groups enabled comparison of these half-sib groups for % consumption and growth. Because data on family relationships are incomplete, analysis of the genetic component of variance was not estimated. Arcsine transformation of percent consumption data was examined (Zar 1984), but had little effect on the distribution or analysis, therefore % consumption data were analysed without transformation.

Results

Experiment 1

Feed consumption by fish in the first study showed a strong family effect (Fig. 1). Feed intake measurements were made on 290 fish over 2 days. Although 310 fish were radiographed, movements by some fish when the radiographic film was exposed caused 20 fish to be left out; they were distributed throughout the families. The weight of feed consumed and % consumption data distributions were not normal, both had a surplus of fish at the lowest consumption categories. Means for weight of feed consumed and % consumption were 2.52 and 2.58, respectively. Both measures of consumption were positively and significantly correlated with body weight. The correlation between body weight with weight of feed consumed was strong and highly significant ($r = 0.74$, $P < 0.001$), the correlation with % consumption was low but highly significant ($r = 0.14$, $P < 0.001$).

The family component of variance was over 18% and over 20% of total phenotypic variance for feed consumed and % consumption, respectively. The variation due to tank differences was smaller, 7% for weight of feed consumed and 9% for % consumption, of total random effect variation and was not included in the estimation of phenotypic variance. The tank by family interaction was less than 0.5% of the phenotypic variance for both measures of feed intake. The remaining ~80% of the phenotypic variance was due to residual variance. The broad

Table 2 Correlations (*r*) between % consumption and measures of growth on individual basis (n = 143) or on family means (n = 31) in experiment 1

Growth trait	Individual *r*	Family mean *r*
*d*weight[1]	0.24**[4]	0.64***
G_w[2]	0.00	0.00
a[3]	0.10	0.32

[1]*d*weight is the change in weight from 24 June to 17 December 1999.
[2]G_w is the specific growth rate for weight defined as (ln $W2$ – ln $W1$) 100/t.
[3]a is a growth index defined as $\log_e G_w = a - 0.371 \ln W_m$.
[4]Significance values are $^*P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

sense heritability estimate was 0.37 ± 0.15 for weight of feed consumed, and 0.41 ± 0.18 for % consumption. Additive genetic effects, dominance effects, maternal effects and common environmental effects are included in this estimate (Becker 1984).

During radiography, approximately 30 fish were accidentally killed by overdose of anaesthetic. Additional fish were lost during growout in ponds and some fish lost PIT tags. Of the 290 fish that were measured for feed intake, 143 fish were subsequently measured for growth in December. Growth and growth rates were typical for this size fish (Table 1). Correlation (r) of individual % consumption with growth measures was low (Table 2); however, the correlation between family means for % consumption and *d*weight was higher and significant (r = 0.64, $P < 0.001$). The correlation between individual weights measured at feed intake measurement and when the fish were harvested was high (r = 0.71, $P < 0.001$).

Experiment 2

Weight of feed consumed and % consumption data of the 2813 individuals in 100 families of the second study, as for the first study, was not normally distributed. The distribution had a surplus of fish with lower feed intake. Means for weight consumed and % consumption were 0.76 and 2.08, respectively (Table 1). The correlation of body weight with weight consumed was r = 0.51 ($P < 0.001$), and body weight with % consumption

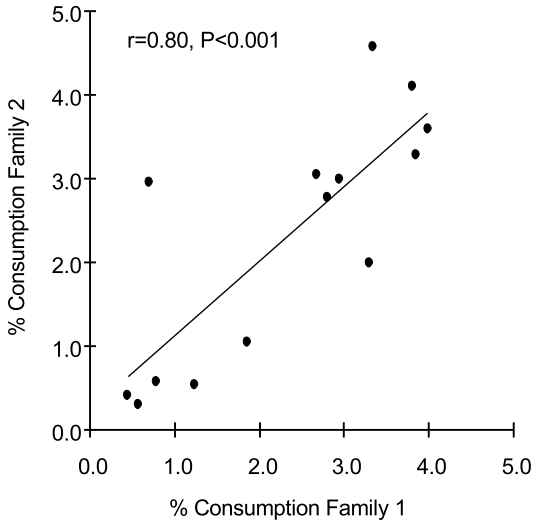

Figure 2 Correlation between the half-sibs from experiment 2. The mean % consumption of one family was correlated with the % consumption of its half-sib family. Sample size was 14 half-sib pairs.

was r = 0.18 ($P < 0.001$). G_w was higher than in experiment one; however, a was similar between the two experiments (Table 1). The correlation between growth from August to October 1999 and % consumption based on family means was r = 0.54 with G_w and 0.58 with a, both correlations were highly significant ($P < 0.001$).

Knowledge of the family membership of 28 full-sib families nested within 14 half-sib groups allowed comparison of the similarity between families with a common sire (Fig. 2); the correlation was high (r = 0.80) and highly significant at $P < 0.001$.

Discussion

These results demonstrated a considerable genetic component for feed intake measured in a single feeding bout. Furthermore, mean % consumption of a family was positively and significantly correlated with growth performance. Measures of % consumption were similar to other feeding studies with channel catfish (Silverstein *et al.* 2000).

A genetic component of feed intake was demonstrated in the first study by the large family effect. The variance component due to full-sib families represents half of the additive genetic variance, half of the dominance variance, maternal effects and environmental effects variance (Becker 1984). Therefore, although there was a significant family

variance component, about 20% of the total phenotypic variance, we cannot estimate the additive genetic variance component alone. A broad sense heritability of 0.37–0.41 for feed intake in channel catfish is similar to heritability for feed intake in poultry (0.34, Chambers *et al.* 1994) and higher than reported for pigs (0.23, Johnson *et al.* 1999). Broiler chickens with higher feed intake had higher body weights, higher yield and lower feed conversion ratios than birds with lower feed intake (Smith, Pesti, Bakalli, Ware & Menten 1998). The correlation among half-sib families found in the second study supports the finding of a sizable genetic component to feed intake measured at a single feeding bout.

In the first experiment the relationship between the one time measurement of feed intake with growth rate, G_w and *a*, in individual fish was not significant; however, the correlation with change in weight, *d*weight, was significant. The reason that *d*weight was correlated with feed intake, but growth rates were not may be because both measures of growth rate adjust for size. G_w expresses daily % change in weight, whereas *a* adjusts for differences in growth rates associated with size of fish. The high correlation of weight at feed intake measurement with weight at harvest for fish in the first experiment ($r = 0.71$) showed that although the biggest fish gained the most weight, they did not grow faster. In the second experiment, growth rates were strongly correlated with % consumption. The fish in the second experiment were younger (1–4 months) than fish in the first experiment (13–20 months), their G_w was higher, and their *a* more variable. This difference suggests that early differences in growth rate have lasting effects on growth potential.

The relationship between family means for % consumption and growth were stronger than those between individual % consumption and growth, indicating that although individual intake varied, family patterns were consistent over time. Taken together with the relatively large family variation for this trait, our results suggest that feed intake should respond to selection and have a correlated response for growth. The associations between consumption and important traits such as feed efficiency and yield have not yet been examined.

The appropriate frequency of measurement for feed intake also has to be determined. In the studies described here, feed intake was measured only once. Multiple measurements would allow examination of the repeatability of the trait, and may result in improved accuracy of individual and family merit estimation. The day-to-day variation in feed intake of fish (e.g. Taylor *et al.* 1999) and the low correlation between consumption and growth measured on individuals compared to families shows that one time measurement of feed intake is not a complete characterization of feed intake ability. Archer *et al.* (1997) showed that different durations of measurement were needed to measure feed intake, growth rate and feed efficiency accurately in cattle.

The mechanisms regulating feed intake and growth in fish are diverse (Peter 1979; LeBail & Boeuf 1997; Silverstein, Shearer, Dickhoff & Plisetskaya 1999b; Boujard, Gelineau, Corraze, Kaushik, Gasset, Coves & Dutto 2000). Himick & Peter (1995) demonstrated a strong relationship between short-term (minutes to hours) feed intake and growth hormone levels in goldfish (*Carassius auratus*). It has also been shown that treatment with exogenous growth hormone enhances long-term (days to weeks) feed intake and growth of channel catfish (Silverstein *et al.* 2000) and many other animals and fish species (reviewed by McLean & Donaldson 1993). These results suggest that growth hormone may be a mechanism for coregulation of growth and feed consumption.

The family component of variation in feed intake is large and promising for selective improvement of feeding and growth in channel catfish. Future studies are needed to determine how and when to measure feed intake most accurately. Work on the physiological regulation of feeding may improve our ability to characterize feed intake potential more completely.

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